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Research Article

Reef Fish Dispersal in the Hawaiian Archipelago: Comparative Phylogeography of Three Endemic Damselfishes

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Endemic marine species at remote oceanic islands provide opportunities to investigate the proposed correlation between range size and dispersal ability. Because these species have restricted geographic ranges, it is assumed that they have limited dispersal ability, which consequently would be reflected in high population genetic structure. To assess this relationship at a small scale and to determine if it may be related to specific reef fish families, here we employ a phylogeographic survey of three endemic Hawaiian damselfishes: *Abudefduf abdominalis*, *Chromis ovalis*, and *Chromis verater*. Data from mitochondrial markers cytochrome *b* and control region revealed low but significant genetic structure in all three species. Combining these results with data from a previous study on *Dascyllus albisella* and *Stegastes marginatus*, all five endemic damselfish species surveyed to date show evidence of genetic structure, in contrast with other widespread reef fish species that lack structure within the Hawaiian Archipelago. Though individual patterns of connectivity varied, these five species showed a trend of limited connectivity between the atolls and low-lying Northwestern Hawaiian Islands versus the montane Main Hawaiian Islands, indicating that, at least for damselfishes, the protected reefs of the uninhabited northwest will not replenish depleted reefs in the populated Main Hawaiian Islands.

1. Introduction

Due to an apparent lack of barriers in the ocean and the potential for larvae to disperse long distances via ocean currents, the previously long-held paradigm has been that there is abundant connectivity and consequently little genetic differentiation between populations of marine organisms [1–3]. However, studies demonstrating self-recruitment and local larval retention indicate that not all marine organisms are exhibiting broad-scale larval dispersal [4–7]. In these circumstances, research has shifted toward understanding the factors mediating connectivity in marine systems and whether there are general patterns related to phylogenetic groups, pelagic larval duration, ecology, or behavior [8–11]. Nevertheless, generalizations have proven elusive.

Isolated oceanic islands provide an excellent opportunity for investigating dispersal in marine organisms. Rates of endemism are markedly high, and since endemic species are usually the products of long periods of isolated local recruitment and reproduction, they serve as model study organisms for understanding dispersal [5]. The general assumption has been that the constrained geographic range sizes of endemic species reflect limited dispersal abilities [9, 12, 13], yet retention-favorable traits are not common characteristics of ocean island endemics [5, 14]. For instance, pelagic larval duration (PLD) is a life history trait that provides an intuitive gauge of dispersal, by the logic that more time spent in the plankton results in greater dispersal and connectivity [15–17]. However, endemic reef fishes do not show a trend toward shorter PLDs relative to widespread congeners, and some studies have shown the opposite [9, 14, 18].

While no diagnostic life history traits related to endemism have been identified, there is support for a positive correlation between dispersal ability and range size [19, 20]. Eble et al. [21] sought to evaluate this relationship through a phylogeographic comparison in the Hawaiian Archipelago

of three surgeonfishes (family Acanthuridae) with different geographic ranges. The Hawaiian endemic was predicted to exhibit less genetic connectivity (more genetic structure) than widespread members of the family. Results supported this hypothesis, with the endemic species demonstrating more, albeit weak, genetic structure than the two species with broader geographic distributions. In the Galapagos Islands, Bernardi et al. [22] surveyed reef fish species with varying range sizes, and again the endemic species demonstrated less genetic connectivity than species with broader distributions. Likewise, in a meta-analysis of tropical reef fishes, the relationship between range size and dispersal potential, as inferred from PLD, was found to vary between oceans, with a significant correlation demonstrated in the Indo-Pacific [20]. This relationship strengthened at higher taxonomic levels and was significant in the damselfishes (Pomacentridae), wrasses (Labridae), and butterflyfishes (Chaetodontidae), indicating that phylogenetic affiliation is a component of this relationship.

Here we assess genetic connectivity across the Hawaiian Archipelago, which is one of the most isolated archipelagoes in the world and has 25% endemism for shore fishes [23, 24]. The archipelago comprises eight Main Hawaiian Islands (MHI), which are "high islands" of volcanic basaltic composition, and ten Northwestern Hawaiian Islands (NWHI), which are mostly "low islands" with coral reefs and sand banks overgrowing subsided basaltic foundations [25]. In this study, we focused on three endemic Hawaiian damselfishes: *Abudefduf abdominalis*, *Chromis ovalis*, and *Chromis verater*. These three species have ranges that span the entire Hawaiian Archipelago, and *C. verater* is also found at Johnston Atoll, about 860 km south of Hawaii. Johnston Atoll is part of the Hawaiian marine biogeographic province because its marine fauna is predominantly Hawaiian [26]. Hence, species that only occur in the Hawaiian Archipelago and Johnston Atoll are still regarded as Hawaiian endemics.

Our study is preceded by a survey of two endemic Hawaiian damselfishes: *Stegastes marginatus* and *Dascyllus albisella* [27]. Ramon et al. [27] analyzed the mitochondrial control region (CR) and found genetic structure in both species, in contrast to the majority of reef fishes surveyed across Hawaii, which show no structure within the archipelago using the mitochondrial marker cytochrome *b* (cyt*b*) [28–31] (but see [32]). Furthermore, one of our study species, *C. verater*, was the subject of a separate study on connectivity between shallow and mesophotic (>30 m) reef habitats [33]. No vertical (depth-related) structure was identified in this species, but the Hawaiian Archipelago was significantly differentiated from adjacent Johnston Atoll (cyt*b*: $\Phi_{ST} = 0.0679$, $P < 0.0001$; CR: $\Phi_{ST} = 0.1156$, $P < 0.0001$).

The three damselfishes surveyed for the current study were chosen because they are abundant throughout the entire archipelago and belong to the sister genera of *Abudefduf* and *Chromis* [34]. This phylogenetic constraint should reduce variable traits among species. There are a total of eight endemic Hawaiian damselfishes, so utilizing results from the previous studies, we are able to examine phylogeographic patterns across five of these species. Given that two Hawaiian endemic damselfishes already show significant genetic structure, we would predict genetic differentiation across the ranges of *A. abdominalis*, *C. ovalis*, and *C. verater* as well, providing more support for a correlation between range size and dispersal ability. Additionally, this finding may indicate that genetic differentiation is typical of endemic Hawaiian damselfishes.

Results from our study also contribute to the conservation of the Hawaiian Archipelago. The NWHI host the Papahānaumokuākea Marine National Monument, one of the largest marine protected areas in the world and the largest in the US. The degree of connectivity between the NWHI and the MHI is of particular interest to the management of marine resources in the archipelago. The vast and uninhabited marine protected area (NWHI), adjacent to a large community that depends on the sea for nutrition (MHI), is postulated to have a spillover effect [35, 36]. Our fine-scale sampling throughout the Hawaiian Islands can illustrate whether the NWHI have the potential to subsidize the overexploited reefs of the MHI.

2. Materials and Methods

2.1. Tissue Collection. Collections of 345 *A. abdominalis*, 412 *C. ovalis*, and 425 *C. verater* specimens (fin clips) were made at 13–15 locations across the Hawaiian Archipelago from 2009 to 2012 (Figure 1). Additional *C. verater* specimens were collected at Johnston Atoll ($N = 47$). Collections were made with pole spears or hand nets while snorkeling or SCUBA diving.

2.2. DNA Extraction, Marker Amplification, and Sequencing. Tissue specimens were preserved in salt-saturated water with 20% DMSO [37]. All of the protocols for DNA extraction, marker amplification, and sequencing are identical to those used in Tenggardjaja et al. [33]. Cyt*b* and mitochondrial CR sequences of *C. verater* generated for Tenggardjaja et al. [33] were used in this study. Additionally, since the lab work for the current study was conducted concurrently with the study on *A. abdominalis* by Coleman et al. [38], cyt*b* sequences of *A. abdominalis* were shared between the authors. Of these sequences, thirteen were identified as hybrids by Coleman et al. [38] and were included in the current study after determining that they did not bias mtDNA analyses. Sequences were aligned using the Geneious aligner and edited using *GENEIOUS R6* (Biomatters, LTD, Auckland, NZ). Alignments of cyt*b* were unambiguous, while CR contained multiple indels of 1-2 bp. Unique haplotypes for each marker were identified in *ARLEQUIN 3.5* [39] and were uploaded to GenBank (KP183329–KP183902, KU842721–KU843500).

2.3. Genetic Diversity and Population Structure Analyses. Haplotype diversity (h) and nucleotide diversity (π) were calculated in *ARLEQUIN*. Population structure was assessed using analyses of molecular variances (AMOVAs) and population pairwise Φ_{ST} comparisons in *ARLEQUIN*. The Φ_{ST} fixation index incorporates genetic distance and ranges from 0 to 1, with low values indicating a lack of genetic structure

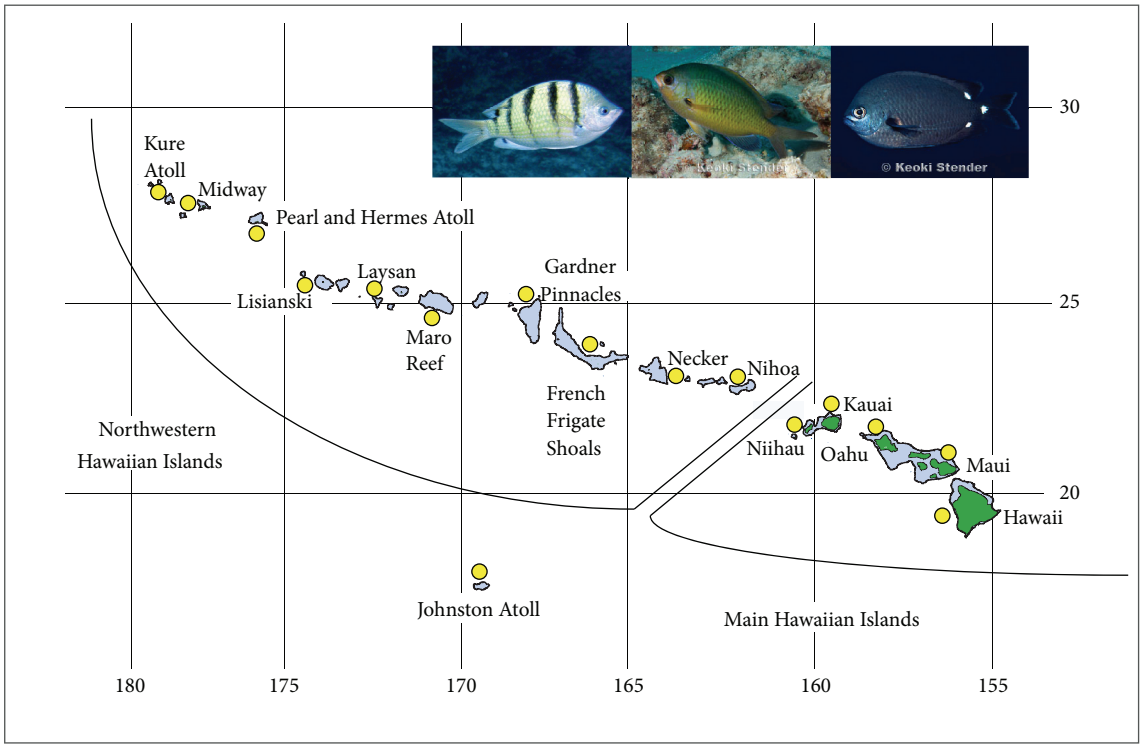

Figure 1: Map of collection locations in the Hawaiian Archipelago and Johnston Atoll for *A. abdominalis*, *C. ovalis*, and *C. verater* (photos left to right). Specimens of all species were collected at each location with the exception of Maro Reef and Johnston Atoll. No *C. verater* specimens were collected at Maro Reef, and only *C. verater* specimens were collected at Johnston Atoll. Yellow dots indicate collection locations, green indicates high islands, and blue indicates low islands and shallow habitat. (Photo credit for *A. abdominalis*: Kim Tenggardjaja. Photo credit for *Chromis* species: Keoki Stender, http://www.marinelifephotography.com/.)

and high values indicating genetic differentiation. Significance of pairwise Φ_{ST} comparisons and AMOVA calculations was tested with 10,000 permutations, and to correct for multiple comparisons, a modified false discovery rate method was implemented [40]. We determined the best model of sequence evolution for each marker in *jMODELTEST 2* [41, 42]. Because the models identified by the Akaike information criterion were not available in *ARLEQUIN*, we selected the Tamura-Nei model as it was the most similar [43]. For *A. abdominalis*, populations at Gardner Pinnacles ($N = 1$) and Nihoa ($N = 1$) were not included in most analyses due to small sample sizes. However, these samples were included in haplotype networks. Parsimony-based haplotype networks for each marker were constructed in *R* using haploNet in the package Pegas 0.5–1 [44]. Haplotype frequencies used in these networks were calculated in *ARLEQUIN*.

To test for a signal of population expansion, Fu's F_s test for neutrality and mismatch distributions was calculated in *ARLEQUIN* with 10,000 permutations [45, 46]. Significant negative F_s values indicate an excess of rare haplotypes, which can be a signal of selection or, more likely, recent population expansion. For cyt*b* data, we fitted the population age parameter τ and pre- and postexpansion population size parameters θ_0 and θ_1 to estimate the time to coalescence [46, 47]. Time to coalescence was calculated with $\tau = 2\mu T$, where T is the age of the population in generations and μ is the fragment mutation rate. Since the generation times of *A. abdominalis*, *C. ovalis*, and *C. verater* are unknown, we conditionally used a generation time of 3 years based on estimates in the damselfish *Chromis chromis* [48]. A mutation rate of 2% per million years between lineages or 1% within lineages for cyt*b* was applied [49].

To avoid making *a priori* assumptions about the locations of genetic barriers, we used the computational geometry approach in *BARRIER 2.2* [50] to visualize genetic barriers in geographic space. Genetic barriers represent changes in genetic composition between sample sites. The software identifies barriers with Voronoi tessellation and Delaunay triangulation, implementing Monmonier's maximum-difference algorithm to compare a distance matrix (e.g., matrix of pairwise population Φ_{ST} values) with a matrix of geographic distances. *A posteriori* AMOVAs subsequently were performed on population groupings identified by *BARRIER*.

Mantel tests were used to test for a correlation between genetic distance and geographic distance. Mantel tests were run in the vegan package in *R* with 10,000 permutations, using matrices of pairwise Φ_{ST} values and geographic distances as calculated by the Geographic Distance Matrix Generator [51, 52]. Mantel tests were performed with matrices that included negative Φ_{ST} and also with negative values converted to zeroes. If AMOVAs detected significant structure among groups comprised of more than one

sample location, partial Mantel tests were run, incorporating a third dissimilarity matrix that took into account the regional structure. Partial Mantel tests can help distinguish whether isolation by distance, or regional population structure, accounts for more genetic variance in data [53].

3. Results

A total of 670 bp of cyt*b* was resolved for *A. abdominalis*, 660 bp for *C. ovalis*, and 719 bp for *C. verater*. For CR, 400 bp was resolved for *A. abdominalis*, 388 bp for *C. ovalis*, and 394 bp for *C. verater*. Summary statistics for number of haplotypes (H), haplotype diversity (h), nucleotide diversity (π), and Fu's F_s are provided in Table 1. For *C. ovalis* and *C. verater*, overall haplotype diversity for cyt*b* was high with $h = 0.9501$ and 0.9077, respectively. Conversely, overall haplotype diversity for cyt*b* in *A. abdominalis* was lower with $h = 0.5865$. For CR, overall haplotype diversity approached saturation for all three species with $h = 0.9955$–0.9997.

All three species had negative and significant Fu's F_s values for both mtDNA markers at most sample locations (Table 1). Summary Fu's F_s values for both markers were negative and significant for all species (cyt*b*: $F_s = -25.6820$ to -29.8590, CR: $F_s = -23.4009$ to -23.7039). Unimodal mismatch distributions in cyt*b* did not indicate significant deviation from a demographic expansion model for any of the species. Based on a generation time of 3 years and a mutation rate of 2% per million years (1% within lineages), mismatch analyses indicated the coalescence times to be on the order of 68,000 years for *A. abdominalis*, 249,000 years for *C. ovalis*, and 163,000 years for *C. verater* (Table 2). Since we used estimates for generation time and mutation rate from other species, calculations for coalescence times are approximations at best.

Overall estimates for Φ_{ST} varied by marker and by species (Table 3). For *A. abdominalis*, Φ_{ST} based on cyt*b* was not significant ($\Phi_{ST} = 0.0063$, $P = 0.0911$), but CR yielded weak yet significant genetic structure ($\Phi_{ST} = 0.0123$, $P = 0.0034$). For *C. ovalis*, fixation indices for both markers showed weak but significant structure (cyt*b*: $\Phi_{ST} = 0.0121$, $P = 0.0047$; CR: $\Phi_{ST} = 0.0059$, $P = 0.0370$). *Chromis verater* had the highest significant Φ_{ST} values across the Hawaiian Archipelago and Johnston Atoll (cyt*b*: $\Phi_{ST} = 0.0232$, $P < 0.0001$; CR: $\Phi_{ST} = 0.0363$, $P < 0.0001$). When analysis was limited to only the Hawaiian Archipelago, the fixation indices for *C. verater* dropped but remained significant (cyt*b*: $\Phi_{ST} = 0.0093$, $P = 0.0197$; CR: $\Phi_{ST} = 0.0115$, $P = 0.0087$).

Pairwise Φ_{ST} comparisons revealed different patterns of genetic structure among the sampling locations for each species (Tables 4, 5, and 6). *Abudefduf abdominalis* had only 6 significant comparisons for cyt*b*, but 19 were significant for CR with 7 of those including comparisons with the sampling location of Niihau, based on $N = 8$. *BARRIER* identified a genetic break between Necker and Niihau, and *a posteriori* AMOVAs confirmed this as a significant break in both markers (cyt*b*: $\Phi_{CT} = 0.0107$, $P = 0.0044$; CR: $\Phi_{CT} = 0.0098$, $P = 0.0123$).

Chromis ovalis had 18 significant comparisons for cyt*b* and 13 for CR, with Pearl and Hermes included in 9 and 4 of these comparisons, respectively. Since most of these comparisons involved populations east of Pearl and Hermes, *a posteriori* AMOVAs simulating a genetic break between Pearl and Hermes and adjacent Lisianski were run, which detected weak yet significant structure for both markers (cyt*b*: $\Phi_{CT} = 0.0121$, $P = 0.0338$; CR: $\Phi_{CT} = 0.0096$, $P = 0.0287$). AMOVAs did not support any of the genetic breaks identified in *BARRIER* for this species.

Chromis verater showed significant differentiation of Johnston Atoll in most pairwise comparisons for cyt*b* and CR (Table 6). Within the Hawaiian Archipelago, the island of Hawaii was significantly different in at least half of the pairwise comparisons for *C. verater* (6 for cyt*b*; 6 for CR). *BARRIER* detected a genetic break between Johnston Atoll and the Hawaiian Archipelago, which was supported by moderate Φ_{ST} values (cyt*b*: $\Phi_{ST} = 0.0679$, $P < 0.0001$; CR: $\Phi_{ST} = 0.1156$, $P < 0.0001$). Also, *BARRIER* identified a genetic break between Maui and the island of Hawaii, and *a posteriori* AMOVAs confirmed this as a significant break (cyt*b*: $\Phi_{CT} = 0.0211$, $P = 0.0194$; CR: $\Phi_{CT} = 0.0352$, $P = 0.0045$).

In addition to examining patterns of genetic structure among sampling locations, we compared the proportion of significant population pairwise Φ_{ST} comparisons: (1) within the NWHI, (2) within the MHI, and (3) between the NWHI and the MHI. The greatest proportion of significant comparisons occurred between locations in the NWHI and MHI (Table 7).

Parsimony-based haplotype networks for cyt*b* were dominated by widely distributed common haplotypes (Figure 2). The network for *A. abdominalis*, which had the lowest haplotype diversity, was dominated by one common haplotype. *Chromis ovalis* and *C. verater*, which had similarly high haplotype diversities, had multiple common haplotypes in the networks. In all species, the most common haplotypes were present at nearly every sampling location. In contrast, the networks for CR in all three species showed an abundance of haplotypes observed in single individuals, as expected with haplotype diversities $h > 0.9900$ (Figure 3). While there did not appear to be much geographic clustering of haplotypes, the CR haplotype network for *C. verater* showed some grouping of Johnston Atoll haplotypes, which supports the genetic differentiation from the Hawaiian Archipelago (Figure 3).

For *C. ovalis* and *C. verater*, the Mantel test for cyt*b* did not indicate isolation by distance, but *A. abdominalis*, the species with the lowest overall population structure, had a significant signal ($r^2 = 0.5308$, $P = 0.0003$). Since AMOVAs with *A. abdominalis* populations grouped into the NWHI and the MHI were significant for both markers, a partial Mantel test for cyt*b* was run accounting for this regional structure. The isolation by distance signal was weaker but still significant ($r^2 = 0.4685$, $P = 0.0005$). For CR, no Mantel tests or partial Mantel tests were significant (data not shown).

Table 1: Molecular diversity indices for *A. abdominalis*, *C. ovalis*, and *C. verater*. Number of individuals (N), number of haplotypes (H), nucleotide diversity (π), haplotype diversity (h), and Fu's F_s are listed for cyt*b* and CR. F_s values in bold are significant ($P < 0.05$). For *A. abdominalis*, populations at Gardner Pinnacles ($N = 1$) and Nihoa ($N = 1$) were not included in most analyses due to small sample sizes.

Sample location	N	H		π		h		Fu's F_s	
		cyt*b*	CR	cyt*b*	CR	cyt*b*	CR	cyt*b*	CR
A. abdominalis									
Hawaiian Archipelago									
Kure	33	7	27	0.0014 ± 0.0011	0.0358 ± 0.0183	0.5833 ± 0.0944	0.9867 ± 0.0111	**−2.9312**	**−8.5606**
Midway	48	7	40	0.0012 ± 0.0010	0.0380 ± 0.0192	0.5408 ± 0.0808	0.9920 ± 0.0061	**−2.9243**	**−18.4921**
Pearl and Hermes	29	7	27	0.0010 ± 0.0009	0.0335 ± 0.0173	0.5222 ± 0.1084	0.9951 ± 0.0106	**−4.3629**	**−13.3511**
Lisianski	16	6	15	0.0011 ± 0.0010	0.0333 ± 0.0177	0.5417 ± 0.1472	0.9917 ± 0.0254	**−3.6160**	**−4.5074**
Laysan	32	12	27	0.0018 ± 0.0013	0.0351 ± 0.0180	0.7157 ± 0.0859	0.9839 ± 0.0144	**−8.7456**	**−9.5195**
Maro Reef	30	11	25	0.0019 ± 0.0014	0.0347 ± 0.0179	0.7448 ± 0.0821	0.9862 ± 0.0129	**−6.9081**	**−7.9587**
French Frigate Shoals	29	11	28	0.0012 ± 0.0010	0.0335 ± 0.0173	0.6207 ± 0.1055	0.9975 ± 0.0099	**−10.2882**	**−16.0317**
Necker	20	7	20	0.0015 ± 0.0011	0.0345 ± 0.0181	0.6421 ± 0.1176	1.0000 ± 0.0158	**−3.6691**	**−9.9856**
Niihau	8	3	8	0.0007 ± 0.0008	0.0248 ± 0.0145	0.4643 ± 0.2000	1.0000 ± 0.0625	−0.9990	−2.2287
Kauai	25	6	25	0.0010 ± 0.0009	0.0393 ± 0.0202	0.4267 ± 0.1216	1.0000 ± 0.0113	**−3.3803**	**−13.4872**
Oahu	28	8	27	0.0015 ± 0.0011	0.0337 ± 0.0174	0.5423 ± 0.1117	0.9974 ± 0.0104	**−4.2214**	**−14.9033**
Maui	28	10	24	0.0013 ± 0.0010	0.0290 ± 0.0151	0.6349 ± 0.1043	0.9868 ± 0.0141	**−8.3239**	**−9.5825**
Island of Hawaii	19	6	17	0.0012 ± 0.0010	0.0343 ± 0.0180	0.5380 ± 0.1330	0.9883 ± 0.0210	**−2.9396**	**−4.6294**
All of Hawaiian Archipelago	345	44	235	0.0013 ± 0.0010	0.0343 ± 0.0171	0.5865 ± 0.0318	0.9955 ± 0.0009	**−29.8590**	**−23.7039**
C. ovalis									
Hawaiian Archipelago									
Kure	29	22	29	0.0046 ± 0.0028	0.0780 ± 0.0391	0.9778 ± 0.0153	1.0000 ± 0.0091	**−20.4731**	**−10.9002**
Midway	38	27	38	0.0050 ± 0.0029	0.0679 ± 0.0339	0.9659 ± 0.0177	1.0000 ± 0.0060	**−25.2805**	**−19.8388**
Pearl and Hermes	37	20	36	0.0049 ± 0.0029	0.0701 ± 0.0349	0.9459 ± 0.0182	0.9985 ± 0.0067	**−11.9549**	**−15.0322**
Lisianski	4	3	4	0.0028 ± 0.0024	0.0526 ± 0.0355	0.8333 ± 0.2224	1.0000 ± 0.1768	0.0062	1.0580
Laysan	33	19	33	0.0040 ± 0.0024	0.0691 ± 0.0346	0.9015 ± 0.0432	1.0000 ± 0.0075	**−13.6652**	**−15.1002**
Maro Reef	28	18	28	0.0054 ± 0.0032	0.0717 ± 0.0361	0.9550 ± 0.0237	1.0000 ± 0.0095	**−10.4982**	**−10.8746**
Gardner Pinnacles	15	13	15	0.0057 ± 0.0034	0.0756 ± 0.0393	0.9714 ± 0.0389	1.0000 ± 0.0243	**−8.3469**	−3.2110
French Frigate Shoals	31	19	31	0.0048 ± 0.0029	0.0691 ± 0.0347	0.9613 ± 0.0191	1.0000 ± 0.0082	**−12.3126**	**−13.5519**
Necker	29	21	29	0.0054 ± 0.0031	0.0689 ± 0.0347	0.9286 ± 0.0418	1.0000 ± 0.0091	**−16.0795**	**−12.0406**
Nihoa	28	21	28	0.0043 ± 0.0026	0.0748 ± 0.0376	0.9418 ± 0.0371	1.0000 ± 0.0095	**−19.6826**	**−10.5918**
Niihau	20	16	19	0.0045 ± 0.0027	0.0665 ± 0.0340	0.9474 ± 0.0435	0.9947 ± 0.0178	**−12.9546**	**−4.1037**
Kauai	29	17	29	0.0043 ± 0.0026	0.0724 ± 0.0363	0.9360 ± 0.0284	1.0000 ± 0.0091	**−10.6489**	**−11.4865**
Oahu	31	19	31	0.0048 ± 0.0028	0.0755 ± 0.0378	0.9462 ± 0.0253	1.0000 ± 0.0082	**−12.3276**	**−12.4146**
Maui	29	21	28	0.0050 ± 0.0029	0.0719 ± 0.0361	0.9729 ± 0.0173	0.9975 ± 0.0099	**−17.0340**	**−8.8047**
Island of Hawaii	31	23	31	0.0053 ± 0.0031	0.0667 ± 0.0335	0.9699 ± 0.0197	1.0000 ± 0.0082	**−19.5568**	**−13.8980**
All of Hawaiian Archipelago	412	144	387	0.0049 ± 0.0028	0.0681 ± 0.0331	0.9501 ± 0.0069	0.9997 ± 0.0002	**−25.6820**	**−23.4292**
C. verater									
Hawaiian Archipelago									
Kure	6	6	6	0.0026 ± 0.0020	0.0683 ± 0.0405	1.0000 ± 0.0962	1.0000 ± 0.0962	**−4.5527**	0.3120
Midway	36	20	36	0.0035 ± 0.0021	0.0760 ± 0.0378	0.9190 ± 0.0322	1.0000 ± 0.0065	**−15.3135**	**−12.9842**
Pearl and Hermes	43	21	41	0.0032 ± 0.0020	0.0817 ± 0.0404	0.9313 ± 0.0220	0.9978 ± 0.0056	**−16.1515**	**−12.6525**
Lisianski	5	4	5	0.0022 ± 0.0018	0.0688 ± 0.0428	0.9000 ± 0.1610	1.0000 ± 0.1265	−1.4048	0.8051

Table 1: Continued.

Sample location	N	H		π		h		Fu's F_s	
		cyt*b*	CR	cyt*b*	CR	cyt*b*	CR	cyt*b*	CR
Laysan	16	11	16	0.0029 ± 0.0019	0.0783 ± 0.0405	0.9083 ± 0.0633	1.0000 ± 0.0221	**−7.3192**	−1.7070
Gardner Pinnacles	12	6	12	0.0021 ± 0.0015	0.0855 ± 0.0452	0.8182 ± 0.0840	1.0000 ± 0.0340	**−2.0878**	−0.0851
French Frigate Shoals	39	18	38	0.0027 ± 0.0018	0.0823 ± 0.0408	0.8920 ± 0.0306	0.9987 ± 0.0062	**−13.6020**	**−14.4092**
Nihoa	36	20	36	0.0036 ± 0.0022	0.0827 ± 0.0411	0.9413 ± 0.0229	1.0000 ± 0.0065	**−14.7456**	**−15.1230**
Niihau	67	34	62	0.0038 ± 0.0023	0.0822 ± 0.0403	0.9439 ± 0.0164	0.9973 ± 0.0033	**−26.6171**	**−24.0938**
Kauai	30	21	27	0.0035 ± 0.0022	0.0797 ± 0.0399	0.9494 ± 0.0276	0.9931 ± 0.0105	**−19.9573**	−3.6324
Oahu	72	31	68	0.0029 ± 0.0018	0.0828 ± 0.0405	0.8901 ± 0.0279	0.9984 ± 0.0026	**−27.2002**	**−24.0863**
Maui	33	17	31	0.0031 ± 0.0019	0.0797 ± 0.0397	0.9072 ± 0.0365	0.9962 ± 0.0086	**−11.9743**	**−8.1731**
Island of Hawaii	30	14	30	0.0028 ± 0.0018	0.0818 ± 0.0409	0.8851 ± 0.0425	1.0000 ± 0.0086	**−8.3701**	**−11.0474**
All of Hawaiian Archipelago	425	104	392	0.0032 ± 0.0020	0.0786 ± 0.0380	0.9152 ± 0.0083	0.9996 ± 0.0002	**−26.4923**	**−23.4322**
Johnston Atoll									
Johnston Atoll	47	11	39	0.0025 ± 0.0016	0.0598 ± 0.0298	0.6920 ± 0.0666	0.9880 ± 0.0082	**−3.4506**	**−11.1614**
Johnston Atoll and Hawaiian Archipelago	472	109	431	0.0032 ± 0.0019	0.0782 ± 0.0378	0.9077 ± 0.0089	0.9995 ± 0.0002	**−26.4557**	**−23.4009**

Table 2: Estimates of τ, pre and post-expansion theta (θ_0 and θ_1), and coalescence time in years (95% confidence limit of τ) for *A. abdominalis, C. ovalis, and C. verater*.

Species	τ	θ_0	θ_1	Coalescence time (years ago)
A. abdominalis	0.918	0	15.716	68,507 (15,746–127,537)
C. ovalis	3.297	0.035	154.375	249,773 (165,152–295,909)
C. verater	2.355	0.011	99999	163,769 (143,394–188,943)

4. Discussion

In accordance with the expected relationship between dispersal ability and range size, the Hawaiian endemic damselfishes *A. abdominalis*, *C. ovalis*, and *C. verater* all demonstrated evidence of genetic differentiation. Although the species differed in terms of the specific patterns of connectivity among locations, in general, there was a trend toward more genetic structure between locations in the NWHI and the MHI, which has implications for the management of marine resources in the Hawaiian Archipelago. Additionally, the genetic breaks exhibited by each species were concordant with previously identified barriers to dispersal in the archipelago [32], providing guidance in defining ecosystem-based management units.

4.1. Population Structure of Hawaiian Endemic Damselfishes. Our genetic survey based on mitochondrial markers cyt*b* and CR revealed that these three endemic damselfishes exhibited low but significant population structure within their ranges. Very few migrants per generation are necessary to prevent genetic differentiation between populations [54], so even weak genetic structure that is statistically significant indicates some restriction to gene flow [55]. For each species in this study, global Φ_{ST} values were significant within the Hawaiian Archipelago, and each species exhibited multiple significant pairwise Φ_{ST} comparisons for both markers. Of the eight endemic Hawaiian damselfishes, the only other species subject to genetic surveys are *D. albisella* and *S. marginatus* [27]. Similar to our results, both of these species had multiple significant pairwise Φ_{ST} comparisons for the mitochondrial control region. Combining results for those two species with results from the current study, all five endemic damselfishes exhibit significant genetic structure, supporting the hypothesis that the restricted ranges of endemic species are coupled with lower dispersal ability. Without data on the three remaining species *Chromis hanui*, *Chromis struhsakeri*, and *Plectroglyphidodon sindonis*, we cannot definitively conclude that all Hawaiian endemic damselfish species demonstrate population subdivision over their range, but so far all results support this trend.

4.2. Anomalies in A. abdominalis. The cyt*b* results for *A. abdominalis* produced several differences from those of *C. ovalis* and *C. verater*: (1) a significant isolation by distance signal, (2) one common haplotype dominating the haplotype network, and (3) lower haplotype diversity. The high mutation rate and higher diversity of the CR may have masked these characteristics in the CR data. While *A. abdominalis*, *C. ovalis*, and *C. verater* share similar life history traits, such as spawning seasonality, feeding behavior, and egg type, they differ in PLD. The PLD for *A. abdominalis* is 17-18 days, while

Table 3: Analyses of molecular variance (AMOVAs) for *A. abdominalis*, *C. ovalis*, and *C. verater* with percent variation (% variation), fixation indices (Φ_{CT} and Φ_{ST}), and associated *P* values. "/" is used to separate different groupings of sampling locations. Bold values are significant ($P < 0.05$). FFS = French Frigate Shoals.

Species	Groupings	cyt*b*						CR					
		Among groups			Within populations			Among groups			Within populations		
		% variation	Φ_{CT}	*P* value	% variation	Φ_{ST}	*P* value	% variation	Φ_{CT}	*P* value	% variation	Φ_{ST}	*P* value
A. abdominalis	All samples				99.37	0.0063	0.0911				98.77	**0.0123**	**0.0034**
	Kure, Midway, Pearl & Hermes, Lisianski, Laysan, Maro Reef, FFS, Necker/Niihau, Kauai, Oahu, Maui, and island of Hawaii	1.07	**0.0107**	**0.0044**	98.81	0.0119	0.081	0.98	**0.0098**	**0.0123**	98.26	**0.0175**	**0.0028**
C. ovalis	All samples				98.79	**0.0121**	**0.0047**				99.41	**0.0059**	**0.0370**
	Kure, Midway, Pearl & Hermes/Lisianski, Laysan, Maro Reef, FFS, Necker, Niihau, Kauai, Oahu, Maui, and island of Hawaii	1.21	**0.0121**	**0.0338**	98.08	**0.0192**	**0.0049**	0.96	**0.0096**	**0.0287**	98.84	**0.0116**	**0.0368**
C. verater	Johnston Atoll and Hawaiian Archipelago												
	All samples				97.68	**0.0232**	**0.0000**				97.06	**0.0363**	**0.0000**
	Johnston Atoll/Hawaiian Archipelago				93.21	**0.0679**	**0.0000**				88.44	**0.1156**	**0.0000**
	Hawaiian Archipelago												
	All samples				99.07	**0.0093**	**0.0197**				98.85	**0.0115**	**0.0087**
	Island of Hawaii/rest of archipelago				97.89	**0.0211**	**0.0194**				96.48	**0.0352**	**0.0045**

Table 4: Population pairwise Φ_{ST} values for *A. abdominalis*. Cyt*b* below the diagonal and CR above. Bold denotes significant values ($P < 0.05$) and $*$ denotes significance after application of the false discovery rate ($P \leq 0.01$). Italic values indicate comparisons between a population from the MHI and a population from the NWHI.

Location	1	2	3	4	5	6	7	8	9	10	11	12	13
(1) Kure	—	−0.0095	**0.0316**	0.0254	−0.0046	0.0012	0.0104	0.0114	***0.0950***	*−0.0070*	***0.0299***	***0.0400****	*0.0154*
(2) Midway	−0.0007	—	0.0147	0.0111	0.0007	−0.0088	0.0162	0.0102	***0.0495***	*0.0009*	*0.0114*	***0.0185***	*0.0031*
(3) Pearl and Hermes	0.0104	−0.0129	—	0.0287	0.0135	0.0053	0.0031	−0.0084	***0.0963***	***0.0268***	***0.0265***	*0.0160*	*0.0157*
(4) Lisianski	0.0059	−0.0086	−0.0217	—	**0.0415**	0.0099	0.0077	−0.0097	*0.0379*	*0.0087*	*0.0165*	*0.0137*	*0.0029*
(5) Laysan	0.0068	0.0042	0.0010	−0.0044	—	0.0082	0.0017	0.0077	***0.1048****	*−0.0008*	***0.0247***	***0.0429****	*0.0111*
(6) Maro Reef	−0.0025	0.0029	0.0049	−0.0054	0.0046	—	0.0148	0.0028	***0.0615***	*0.0019*	*−0.0056*	*0.0035*	*−0.0029*
(7) French Frigate Shoals	0.0232	0.0129	−0.0089	−0.0170	0.0069	0.0087	—	−0.0101	***0.0945****	*−0.0059*	***0.0283***	***0.0245***	*0.0073*
(8) Necker	0.0174	0.0051	−0.0082	−0.0273	0.0095	−0.0063	−0.0065	—	***0.0737***	*−0.0005*	*0.0131*	*−0.0021*	*0.0087*
(9) Niihau	*0.0125*	*0.0138*	*0.0033*	*−0.0121*	*−0.0111*	*−0.0203*	*−0.0372*	*−0.0028*	—	**0.0543**	0.0343	0.0289	0.0171
(10) Kauai	*0.0161*	*0.0108*	*−0.0011*	*−0.0004*	*0.0004*	*−0.0028*	*0.0030*	***0.0210***	−0.0042	—	0.0090	0.0184	−0.0033
(11) Oahu	***0.0420****	***0.0340***	*0.0160*	*0.0034*	*0.0150*	*0.0165*	*0.0010*	*0.0088*	−0.0236	0.0125	—	0.0030	−0.0054
(12) Maui	***0.0377***	***0.0261***	*0.0141*	*−0.0050*	*0.0134*	*0.0063*	*0.0009*	*−0.0095*	−0.0181	0.0064	−0.0047	—	0.0004
(13) Island of Hawaii	*0.0110*	*0.0217*	*0.0134*	*0.0069*	*0.0070*	*−0.0131*	*−0.0044*	***0.0232***	−0.0468	−0.0089	0.0083	0.0104	—

Table 5: Population pairwise Φ_{ST} values for *C. ovalis*. Cyt*b* below the diagonal and CR above. Bold denotes significant values ($P < 0.05$) and $*$ denotes significance after application of the false discovery rate ($P \leq 0.01$). Italic values indicate comparisons between a population from the MHI and a population from the NWHI.

Location	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
(1) Kure	—	0.0088	0.0043	0.0072	0.0077	0.0045	−0.0050	0.0086	**0.0320**	0.0073	***0.0260***	*0.0045*	*0.0082*	*0.0018*	*0.0147*
(2) Midway	0.0062	—	0.0029	0.0344	0.0019	0.0046	−0.0033	−0.0066	**0.0379***	−0.0029	***0.0232***	*−0.0017*	*0.0120*	*−0.0054*	*0.0134*
(3) Pearl and Hermes	**0.0275**	0.0034	—	0.0595	0.0139	0.0098	0.0090	0.0038	**0.0557***	0.0153	***0.0488****	*−0.0107*	***0.0220***	*0.0120*	***0.0283***
(4) Lisianski	**0.1199**	0.0663	**0.1588**	—	−0.0212	−0.0022	−0.0217	0.0138	−0.0460	−0.0173	*−0.0241*	*0.0508*	*−0.0269*	*−0.0336*	*−0.0374*
(5) Laysan	0.0022	0.0010	**0.0446***	0.0977	—	0.0004	−0.0075	−0.0014	0.0048	−0.0112	*0.0026*	*0.0130*	*−0.0047*	*−0.0139*	*−0.0097*
(6) Maro Reef	0.0090	−0.0074	0.0198	0.0671	−0.0087	—	−0.0092	−0.0021	**0.0221**	−0.0120	*0.0149*	*0.0076*	*0.0057*	*0.0010*	*0.0119*
(7) Gardner Pinnacles	0.0141	−0.0005	0.0317	0.0340	0.0033	−0.0093	—	−0.0155	0.0041	−0.0204	*−0.0086*	*−0.0047*	*−0.0122*	*−0.0152*	*−0.0004*
(8) French Frigate Shoals	0.0197	−0.0087	0.0120	0.0942	0.0131	0.0018	0.0004	—	**0.0206**	−0.0122	*0.0084*	*−0.0066*	*0.0007*	*−0.0062*	*0.0084*
(9) Necker	**0.0326**	0.0154	**0.0578***	0.0286	−0.0040	−0.0050	−0.0006	**0.0321**	—	0.0123	*−0.0036*	***0.0479****	*0.0034*	*0.0029*	*0.0082*
(10) Nihoa	0.0234	0.0042	**0.0586***	0.0319	−0.0074	−0.0024	−0.0064	0.0119	0.0024	—	*−0.0049*	*0.0061*	*−0.0095*	*−0.0125*	*−0.0036*
(11) Niihau	***0.0396***	*0.0284*	***0.0781****	*0.0346*	*0.0092*	*0.0051*	*0.0162*	***0.0467***	*−0.0151*	*0.0026*	—	**0.0416***	−0.0064	−0.0023	−0.0075
(12) Kauai	*0.0071*	*−0.0077*	*−0.0094*	***0.1716***	*0.0203*	*0.0063*	*0.0137*	*−0.0038*	***0.0414***	***0.0364***	**0.0691***	—	0.0119	0.0042	**0.0255**
(13) Oahu	*0.0102*	*0.0030*	***0.0419***	*0.0346*	*−0.0163*	*−0.0053*	*0.0029*	*0.0145*	*−0.0072*	*−0.0033*	−0.0027	0.0234	—	−0.0055	−0.0001
(14) Maui	*0.0208*	*−0.0026*	***0.0431***	*0.0404*	*−0.0047*	*−0.0008*	*−0.0166*	*0.0055*	*0.0035*	*−0.0047*	0.0213	0.0217	0.0014	—	−0.0083
(15) Island of Hawaii	*0.0116*	*−0.0005*	***0.0369***	*0.0229*	*−0.0087*	*−0.0081*	*−0.0065*	*0.0071*	*−0.0043*	*−0.0086*	−0.0091	0.0202	−0.0173	−0.0052	—

Table 6: Population pairwise Φ_{ST} values for *C. verater*. Cyt*b* below the diagonal and CR above. Bold denotes significant values ($P < 0.05$) and $*$ denotes significance after application of the false discovery rate ($P \leq 0.01$). Italic values indicate comparisons between a population from the MHI and a population from the NWHI.

Location	1	2	3	4	5	6	7	8	9	10	11	12	13	14
(1) Kure	—	−0.0259	−0.0317	0.0116	−0.0169	−0.0355	−0.0113	0.0273	*−0.0334*	*−0.0325*	*−0.0214*	*−0.0243*	*0.0180*	**0.1985***
(2) Midway	−0.0556	—	0.0102	−0.0081	−0.0125	−0.0071	0.0235	**0.0554***	*−0.0001*	*−0.0120*	*0.0003*	*−0.0055*	***0.0637****	**0.1465***
(3) Pearl and Hermes	−0.0573	−0.0104	—	0.0334	0.0125	−0.0142	−0.0026	0.0126	*−0.0043*	*−0.0007*	*0.0020*	*0.0027*	*0.0163*	**0.1367***
(4) Lisianski	**0.2098**	**0.1159**	**0.1436**	—	−0.0189	0.0084	0.0396	0.0843	*0.0238*	*−0.0061*	*0.0263*	*0.0052*	***0.1083***	**0.1916***
(5) Laysan	−0.0140	−0.0086	0.0040	0.0528	—	0.0057	0.0326	**0.0708**	*0.0035*	*−0.0016*	*0.0036*	*−0.0061*	*0.0792*	**0.1285***
(6) Gardner Pinnacles	−0.0051	−0.0101	−0.0187	**0.2970***	0.0312	—	−0.0155	0.0124	*−0.0061*	*−0.0160*	*−0.0047*	*−0.0115*	*0.0052*	**0.1591***
(7) French Frigate Shoals	−0.0138	0.0118	−0.0027	**0.2386***	**0.0448**	−0.0371	—	0.0051	*0.0015*	*0.0123*	*0.0089*	*0.0078*	*0.0096*	**0.1257***
(8) Nihoa	−0.0179	**0.0247**	0.0125	**0.1414**	0.0254	−0.0139	0.0104	—	***0.0277***	***0.0453***	***0.0394****	***0.0501****	*−0.0048*	**0.1799***
(9) Niihau	*−0.0520*	*0.0024*	*−0.0050*	***0.1425****	*0.0118*	*−0.0174*	*−0.0019*	*0.0089*	—	−0.0022	−0.0010	0.0009	**0.0343**	**0.1291***
(10) Kauai	*−0.0490*	*−0.0078*	*−0.0102*	***0.1577****	*0.0055*	*−0.0145*	*0.0016*	***0.0280***	−0.0023	—	−0.0037	−0.0065	**0.0555**	**0.1370***
(11) Oahu	*−0.0476*	*0.0003*	*−0.0061*	***0.1861****	*0.0146*	*−0.0100*	*0.0040*	***0.0271****	−0.0013	−0.0079	—	−0.0108	**0.0521***	**0.1047***
(12) Maui	*−0.0536*	*−0.0050*	*−0.0093*	***0.1569***	*0.0137*	*0.0001*	*0.0104*	***0.0351***	0.0026	−0.0060	−0.0072	—	**0.0621***	**0.1087***
(13) Island of Hawaii	*0.0104*	***0.0416***	*0.0215*	***0.2449****	***0.0690***	*−0.0231*	*−0.0061*	*−0.0009*	0.0144	**0.0380**	**0.0367**	**0.0411**	—	**0.2140***
(14) Johnston Atoll	0.0295	**0.0473***	**0.0699***	**0.2578**	**0.0591**	**0.0941**	**0.1045***	**0.1287***	**0.0743***	**0.0375**	**0.0651***	**0.0589***	**0.1563***	—

Table 7: Percentage of significant ($P < 0.05$) pairwise Φ_{ST} comparisons within the NWHI, within the MHI, and between the NWHI and MHI for *A. abdominalis, C. ovalis, and C. verater*, based on cyt*b* and CR sequence data.

Species	cyt*b*				CR			
	Total number of significant comparisons	Within NWHI	Within MHI	Between NWHI and MHI	Total number of significant comparisons	Within NWHI	Within MHI	Between NWHI and MHI
A. abdominalis	6	—	—	100%	19	11%	5%	84%
C. ovalis	18	44%	6%	50%	13	38%	15%	46%
C. verater	21	38%	14%	48%	12	17%	33%	50%

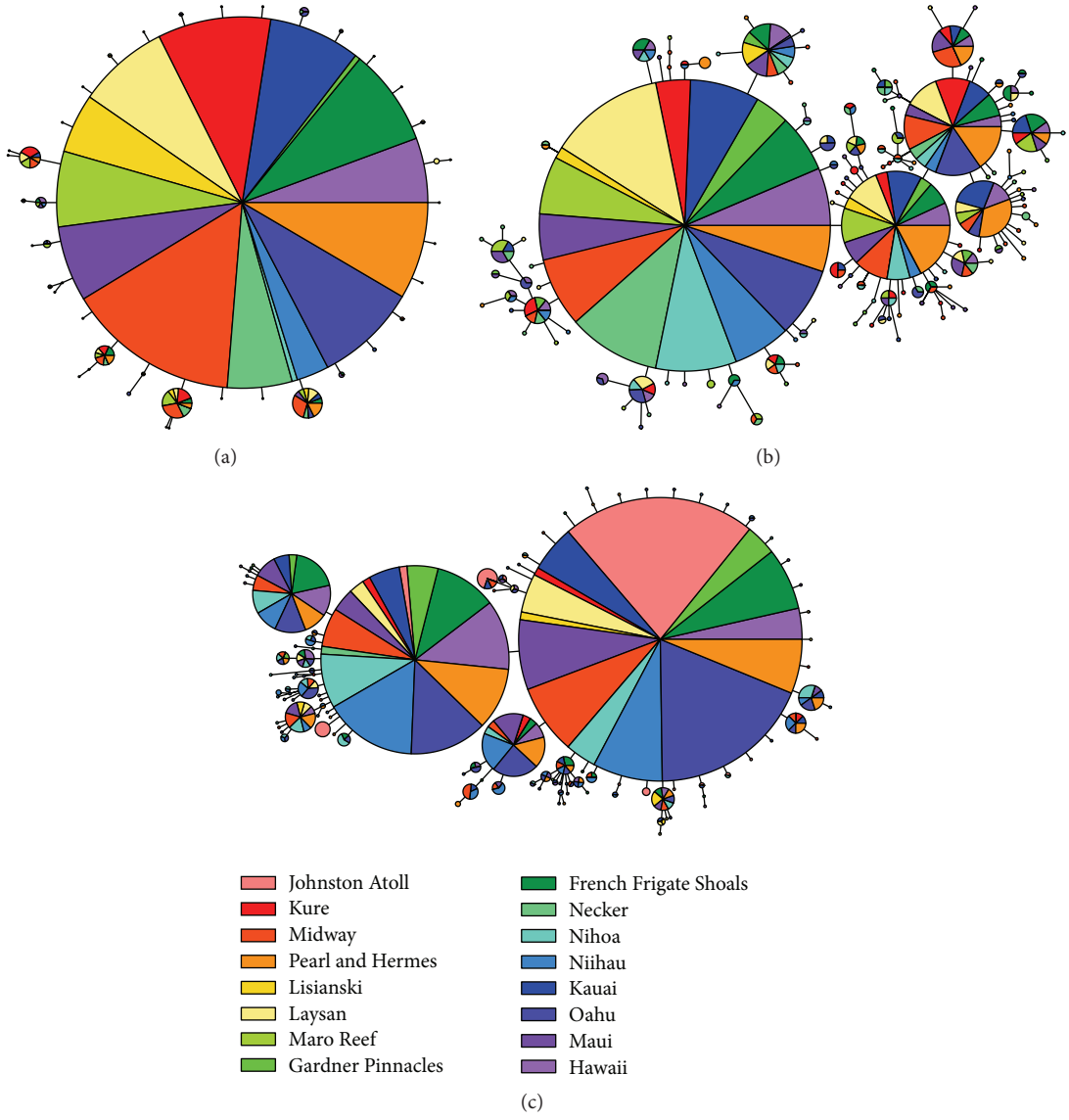

Figure 2: Parsimony-based haplotype networks using cyt*b* sequence data for (a) *A. abdominalis*, (b) *C. ovalis*, and (c) *C. verater*. Each circle represents a haplotype and is proportional to the frequency of that haplotype. Length of branches is proportional to number of mutations. Networks are color-coded by sampling location and are not scaled relative to each other.

the PLDs for *C. ovalis* and *C. verater* are estimated to be 30 days and as long as 3 months, respectively [13, 56]. The isolation by distance signal for *A. abdominalis* may result from a shorter PLD and thus lower dispersal [17], yet the relationship between PLD and dispersal distance remains controversial [57–59]. One notable result from our data sets is a rank order wherein the species with the longest PLD (*C. verater*) has the most population structure and the species with the shortest PLD (*A. abdominalis*) has the least structure, contrary to expectations.

In addition to PLD, the depth ranges for the *Chromis* species (5–199 m) differ from that of *A. abdominalis* (1–50 m). Sea level fluctuations during the Pleistocene reduced coastal habitat in the Hawaiian Archipelago by 75%, likely fragmenting populations of many shallow-water marine species [60]. *Chromis ovalis* and *C. verater* may have retreated to refugia in the deeper parts of their depth range, while *A. abdominalis* may have been more susceptible to these changes in sea level [61]. As observed in other marine taxa [60], the refugia populations of the *Chromis* species may have become genetically differentiated over time and subsequently reestablished connectivity once sea levels rose, resulting in haplotype networks comprised of several common haplotypes. Conversely, in *A. abdominalis*, the network is dominated by a single haplotype, and its lower haplotype diversity may reflect a population bottleneck following sea level change and subsequent population expansion, a pattern found in multiple marine taxa [60]. Significant negative Fu's F_s values, unimodal mismatch distributions, and shallow coalescence times reinforce that all three species have experienced recent population expansions, possibly as a result of past fluctuations in climate and sea level.

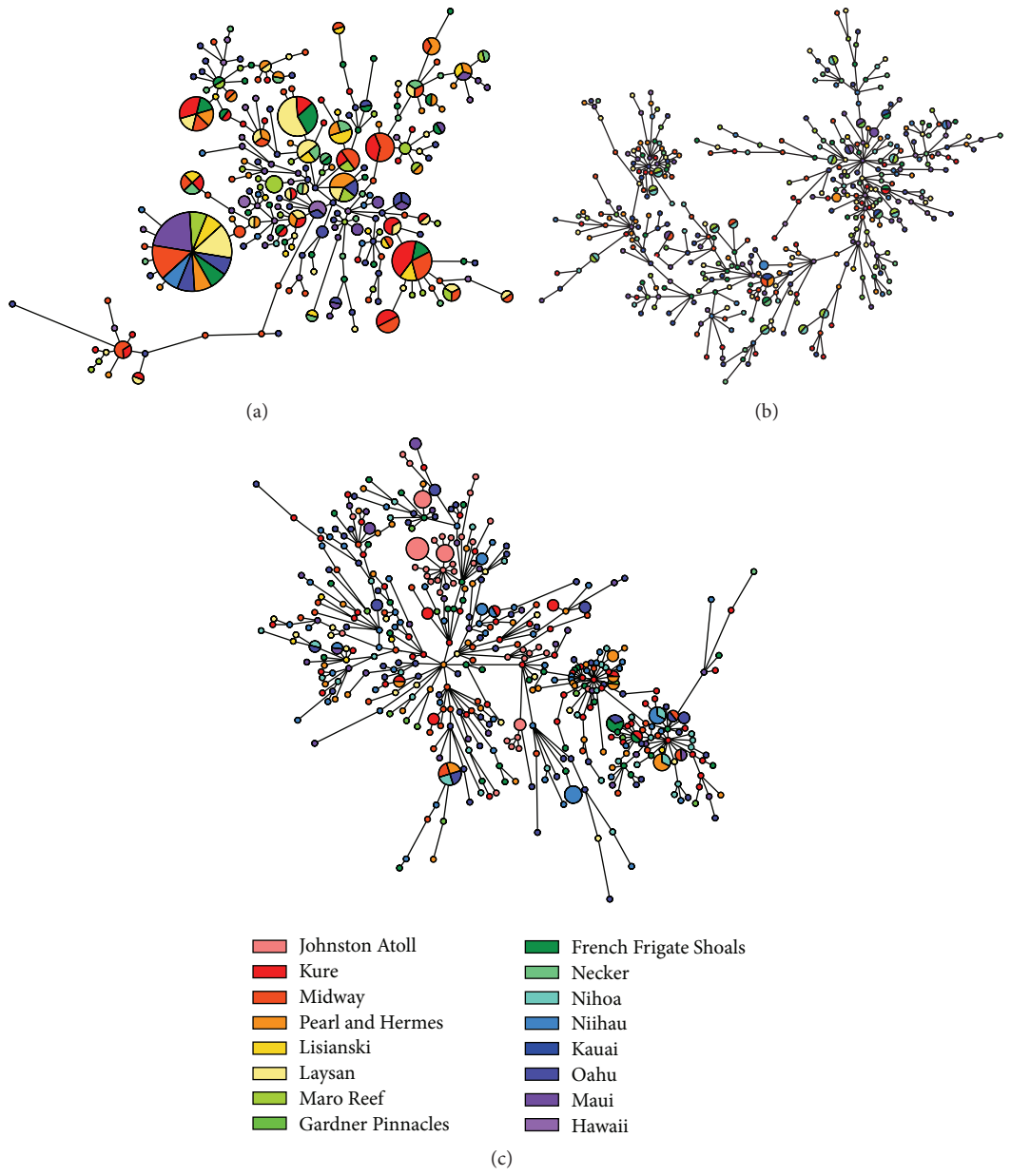

FIGURE 3: Parsimony-based haplotype networks using CR sequence data for (a) *A. abdominalis*, (b) *C. ovalis*, and (c) *C. verater*. Each circle represents a haplotype and is proportional to the frequency of that haplotype. Length of branches is proportional to number of mutations. Networks are color-coded by sampling location and are not scaled relative to each other.

4.3. Phylogeographic Patterns of Hawaiian Endemic Reef Fishes. Since multiple genetic surveys exist for endemic Hawaiian reef fishes, we can compare results to investigate the relationship between range size and dispersal ability. Lester and Ruttenberg [20] found a correlation between PLD and range size for certain reef fish families but not for others. The current study demonstrates that most Hawaiian endemic species in the Pomacentridae exhibit genetic structure. The Hawaiian grouper, *Hyporthodus quernus*, is the only member of Serranidae endemic to the Hawaiian Archipelago and Johnston Atoll. Population pairwise comparisons for CR and nuclear microsatellite markers demonstrated low but significant structure within the Hawaiian Islands [62]. In contrast, the widespread grouper *Cephalopholis argus* showed no population structure from the central Pacific (Line Islands) to northeastern Australia, a distance of about 8000 km [63]. In the surgeonfishes (Acanthuridae), the Hawaiian endemic *Ctenochaetus strigosus* exhibited low to moderate genetic structure in population pairwise comparisons for cyt*b* [21]. The surgeonfish *Zebrasoma flavescens*, which occurs across the NW Pacific but is most abundant in the Hawaiian Archipelago, shows multiple population breaks within the archipelago [64]. In the same family, *Acanthurus nigroris*, which was reclassified as a Hawaiian endemic [65],

showed low yet significant population structure in pairwise comparisons and a significant global Φ_{ST} value across its range, driven by the Johnston Atoll specimens [30]. In the wrasses (Labridae), *Halichoeres ornatissimus* only exhibited significant genetic differentiation in pairwise comparisons with Johnston Atoll and, otherwise, did not show significant structure within the Hawaiian Islands [66]. Hawaiian endemic butterflyfishes (Chaetodontidae) also lacked population structure, with cyt*b* data revealing no genetic structure for *Chaetodon fremblii*, *Chaetodon miliaris*, or *Chaetodon multicinctus* [28]. Though some Hawaiian (or North Pacific) endemics show structure and others do not, this should be interpreted against findings for widespread Indo-Pacific fishes that occur in Hawaii, which almost uniformly show a lack of population structure across this archipelago [29, 31, 67–71].

Besides the Pomacentridae, genetic surveys of Hawaiian endemics are only available for one to three species within other reef fish families, making it difficult to draw robust conclusions regarding whether taxonomic family is a good predictor of the relationship between range size and dispersal ability. Superficially, there appears to be a trend in the families that have genetic data for more than one Hawaiian endemic species. Genetic structure is observed in five endemic damselfishes and in three surgeonfishes, though structure in *A. nigroris* is inconsistent. The three endemic butterflyfishes lacked genetic structure, but surveys of other butterflyfishes indicate that extensive dispersal is a feature of these taxa [72–76]. Additional genetic surveys of Hawaiian endemic reef fishes would provide interesting perspective on whether there is consistency in the relationship between range size and dispersal ability at the taxonomic family level.

4.4. Connectivity between the NWHI and the MHI and Concordant Genetic Breaks in the Hawaiian Archipelago. While individual patterns of genetic connectivity among sampling locations varied by species, our study found that that there was more genetic structure between the NWHI and the MHI than within either region (Table 7). Additionally, AMOVAs for *A. abdominalis* exhibited a significant genetic break between these two regions (Table 3). Results for *D. albisella* and *S. marginatus* also supported this trend with 57% and 50% of respective significant pairwise comparisons occurring between the NWHI and the MHI [27]. Though *A. abdominalis*, *C. ovalis*, and *C. verater* demonstrated weak genetic structure, there is a clear signal of isolation between these two regions. Since these species are only found in the Hawaiian Islands and Johnston Atoll, management plans should take into account spatial patterns of connectivity exhibited by endemic species, in order to preserve the unique biodiversity within this region.

Multispecies genetic surveys are useful for implementing ecosystem-based management and highlighting potential management units [77, 78]. This study detected several significant genetic breaks in the archipelago: (1) between the NWHI and the MHI (*A. abdominalis*), (2) east of Pearl and Hermes (*C. ovalis*), and (3) between Maui and the island of Hawaii (*C. verater*). These breaks are consistent with three previously identified barriers in the Hawaiian Archipelago. Toonen et al. [32] compared genetic surveys of 27 taxonomically diverse species on Hawaiian coral reefs and found four concordant barriers to dispersal, based primarily on reef invertebrates. Agreement between those breaks and the ones in our study contributes to the proposal that these barriers delineate potential zones of resource management. Moreover, the consistency in genetic breaks across different taxonomic groups reinforces the conclusion that abiotic factors play a role in limiting connectivity within the archipelago.

5. Conclusions

Based on the results from this study and Ramon et al. [27], the five Hawaiian endemic damselfishes surveyed to date exhibit genetic structure across their ranges. This finding supports a relationship between range size and dispersal ability. However, this would be more strongly supported if widespread damselfish species demonstrated lower genetic structure across the same geographic range as the endemic species. Our review of genetic surveys of Hawaiian endemic reef fishes indicates that the presence of genetic structure in endemic species may be specific to particular taxonomic families. Genetic data on widespread damselfish species in the Hawaiian Archipelago would be useful in teasing apart this trend from the possibility that the life history traits of damselfishes simply predispose them to showing genetic structure [79]. (However, some studies already have demonstrated a lack of structure in damselfish species [22, 78, 80].) Since our study was limited to the Hawaiian Archipelago and Johnston Atoll, it is difficult to extend our conclusions to other archipelagos, as place-specific abiotic factors (e.g., oceanography, geologic history) undoubtedly contribute to restricting the dispersal of endemic species.

Our results on the Hawaiian endemics *A. abdominalis*, *C. ovalis*, and *C. verater* not only reinforce previously identified genetic breaks in the Hawaiian Archipelago, but also illustrate a general trend in connectivity in endemic Hawaiian reef fishes. The preservation of marine biodiversity inherently calls for a better understanding of connectivity patterns in endemic species. The genetic structure between locations in the NWHI and the MHI in our study species and in Ramon et al. [27] indicates that the protected status of the Papahānaumokuākea Marine National Monument may not result in replenishment of depleted reef resources in the MHI. Therefore, taking measures to ensure connectivity between protected areas in the MHI will aid in maintaining the biodiversity unique to this archipelago.

Competing Interests

The authors declare that they have no competing interests.

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